Do sub-Arctic winter moth populations in coastal birch forest exhibit spatially synchronous dynamics?

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Summary

1. Populations of cyclic forest insects are known to exhibit large-scale spatially synchronous dynamics. Region-wide climatic disturbances, the Moran effect, have often been invoked as the mechanism underlying this synchrony. However, no previous study has been designed specifically to examine spatial population dynamics more closely and to evaluate underlying mechanisms.

2. We perform a study on winter moth populations in sub-Arctic birch forest, where habitat discontinuity was included in the study design, to evaluate if dispersal barriers would act to decouple dynamics. All the study populations were situated in the same climatic region where 10-year population cycles have been known to prevail. The total spatial extent of the study was smaller than the spatial scale of synchronous dynamics reported from previous studies on cyclic insects.

3. We found that moth populations had mainly synchronous dynamics within sites consisting of 1·8 km transects in prime moth habitats (mature birch forest) and within a large island with continuous birch forest. However, sites on different islands could be maximally out of phase.

4. These results suggest that climate was not synchronizing winter moth populations in this ecosystem and that biotic mechanisms are probably involved.

5. Our study highlights the value of performing studies with a particularly dedicated design for elucidating the patterns and mechanisms of spatio-temporal population dynamics.

Key-words: climate, dispersal barriers, insect population cycles, Moran effect, study design.

Journal of Animal Ecology (2004) **73**, 1129–1136

Introduction

Studies of population dynamics have increasingly emphasized two spatial aspects (Bascompte & Solé 1998; Bjørnstad, Ims & Lambin 1999; Lundberg *et al.* 2000). One aspect, which has been emphasized particularly in some species of small rodents and geometrid moths (Klemola *et al.* 2002), is that different geographical regions may harbour populations of the same species with qualitatively different types of dynamics. Notably in Europe there is a northern 'cyclic region' with high amplitude peak years occurring at regular intervals, and more southern 'non-cyclic regions' with low amplitude, irregular population fluctuations. Such large-scale differences in population-dynamics patterns

have been used to infer processes underlying the dynamics (Hansson & Henttonen 1988; Klemola *et al.* 2002). The other aspect regards the extent of spatially synchronous dynamics, which has now been investigated in many species (Hanski & Woiwod 1993; Ranta, Kaitala & Lundberg 1998; Koenig 1999; Paradis *et al.* 2000). It has been concluded that population synchrony is taxonomically and geographically widespread (Hudson & Cattadori 1999; Koenig 1999), but there are large differences among species and geographical regions with respect to how pronounced synchrony is locally and how fast it decays with distance (Kendall *et al.* 2000). In some species there is evidence for continent-wide synchrony (Hawkins & Holyoak 1998), while synchrony in other species is mainly a local phenomenon (Steen, Ims & Sonerud 1996). It seems, however, that populations with cyclic dynamics stand out as those cases with the most pronounced and large-scale synchrony (Barbour 1988; Bjørnstad 2000; Kendall *et al.*

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2000; Liebhold & Kamata 2000). This indicates that those mechanisms generating population cycles and those generating synchrony either are the same or are at least interacting (Kendall *et al.* 2000).

Populations of the two geometrid moth species (*Epirrita autumnata* Bkh.) (autumnal moth) and (*Operophtera brumata* L.) (winter moth) in sub-Arctic and subalpine birch forests of Fennoscandia are well known for their approximately 10 years population cycles (Tenow 1972, 1996; Haukioja *et al.* 1988; Hogstad 1997; Bylund 1999; Neuvonen, Niemelä & Virtanen 1999; Klemola *et al.* 2002). Besides the broad geographical distribution of areas with and without population cycles (Ruohomäki *et al.* 2000; Klemola *et al.* 2002), the spatial aspect of geometrid moth cycles in the birch forest ecosystem has been relatively little emphasized. Tenow's (1972) seminal survey of known outbreak years in Fennoscandia covering a period of more than 100 years indicated that outbreaks in both moth species could encompass large tracts of suitable habitat (i.e. birch forests). Mainly on this basis large-scale spatial synchrony has been concluded to be the rule for cyclic birch forest geometrids (Bylund 1999; Ruohomäki *et al.* 2000; Tanhuanpää *et al.* 2002). However, besides the qualitative survey of Tenow (1972), there have been no studies devoted specifically to the spatial population dynamics of the two geometrid moth species in the birch-forest ecosystem. The possibility to conduct such

studies has been hampered by a scarcity of quantitative data on population densities with an appropriate spatial coverage.

Because qualitative surveys may be fraught with many caveats (see Tenow 1972 for a thorough discussion) in this paper we raise the question of whether the conventional wisdom about synchronous dynamics of birch-forest geometrids holds closer scrutiny in terms of more detailed quantitative data. For this purpose we report from an ongoing project that is aimed specifically at exploring the spatial dynamics of geometrid moths. Our study is conducted in coastal, sub-Arctic birch forests of northern Norway where the winter moth in particular is well known to exhibit 10-year population cycles (Tenow 1972; Bylund 1999; Neuvonen *et al.* 1999). These forests provide excellent opportunities for studying spatio-temporal dynamics of forest-dwelling organisms as they typically form narrow belts between the sea and higher altitude treeless habitat (forest line at 300–500 m in the study area), which simplifies the spatial dimension of the populations. Moreover, the forest belts are discontinued by fjords or are located on different large islands so that the dynamics of populations separated by dispersal barriers can be analysed (see Fig. 1). Adjacent sites separated by barriers are so closely situated (< 10 km) that they are exposed to virtually the same climate. Such a context can be used strategically to distinguish between climate
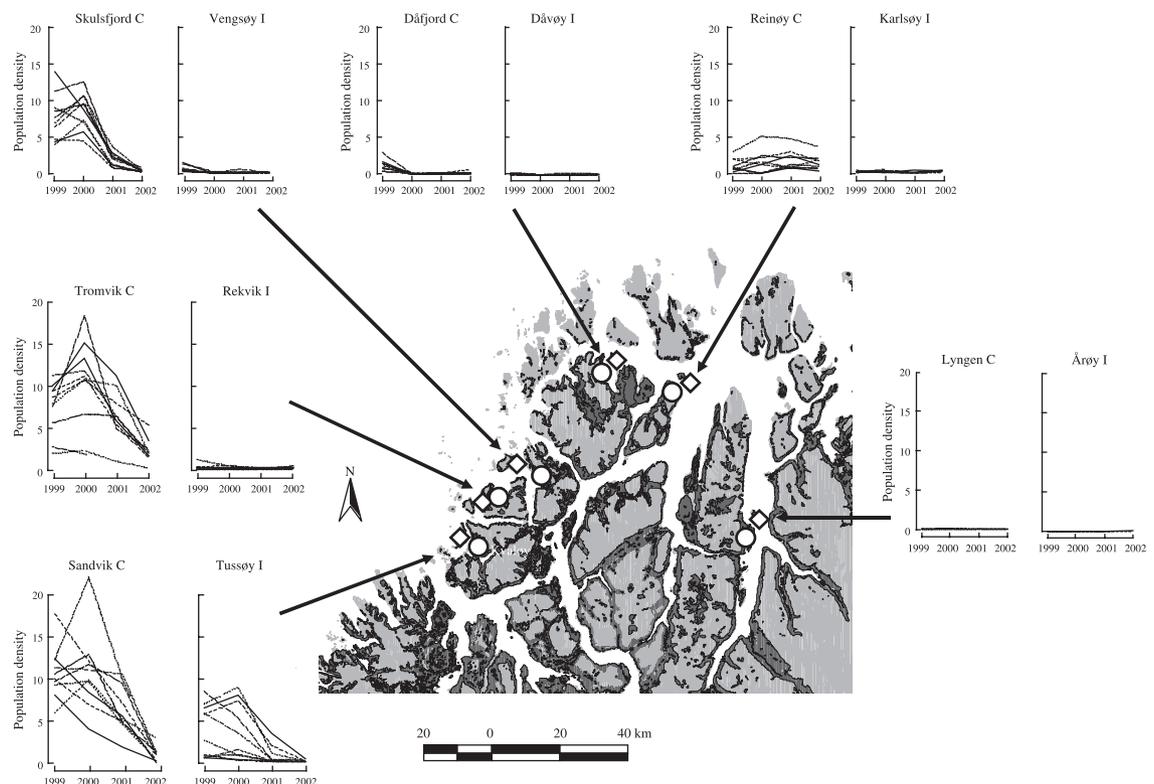

Fig. 1. The six pairs of sites in the coastal districts of Troms county in northern Norway where winter moth populations were censused during 1999–2002. The population trajectories of the 10 local stations per site are shown on as number of larvae per twig at a linear scale. The letters after the site names indicate whether the site was on the mainland or a large island (C: continent) or on a smaller island (I). On the map island sites are marked with diamonds, mainland sites with dots. Dark terrestrial areas on the map denote birch forest, while light areas denote treeless, alpine habitats.

and dispersal as synchronizing factors (Adler 1994; Grenfell *et al*. 1998; Bjørnstad *et al*. 1999; Krebs *et al*. 2002).

Although studies of the dynamics of cyclic populations for many purposes need to span a longer time period than the period of a cycle (i.e. 10 years for the focal moth species), the degree of synchronous dynamics can be evaluated from more short-term data (e.g. Bondrup-Nielsen & Ims 1988; Erlinge *et al*. 1999; Laakkonen *et al*. 2001). In fact, an evaluation of spatial synchrony requires only that the same measure of population growth rate can be compared among populations. For cyclic populations, identifying and comparing the phase among sites at any given time would be sufficient to verify the prevalence of synchrony. Here we use this latter approach on our 4-year data sets on winter moth population dynamics from multiple sites in northern Norway. Our results appear to contradict the notion that cyclic moth species exhibit spatial synchrony due to the Moran effect (Tenow 1972; Berryman 1996; Ruohomäki *et al*. 2000; Tanhuanpää *et al*. 2002), at least in coastal sub-Arctic birch forest.

Methods

The project was carried out in the coastal districts of Troms county, northern Norway (69°30′ to 70°03′N; 18° to 20°E). The climate in this area is oceanic with relatively mild winters (average January temperature −2 to −5 °C) and cool, wet summers (average July temperature 12–13 °C). Twelve main study sites in mature birch forest were selected. The 12 study sites were arranged spatially in six pairs so that one site was on the mainland or a very large island (hereafter termed continent) and one on a medium-sized island (hereafter termed island) (Fig. 1). Except for one locality (Rekvik), which is a forest island isolated from the 'continental forest' by treeless alpine habitats, the other islands were true islands surrounded by sea. The straight-line distance between the continent and the island within a pair ranged from 4 to 9 km and always included a stretch of more than 1·5 km of open sea (or mountain habitat in the case of Rekvik), which probably constitute an efficient barrier for ballooning larvae (Edland 1971). The straight-line distance between the two nearest sites from two different pairs ranged from 13 to 42 km.

At each site we established one 1·8-km transect running through continuous typical winter moth habitat (i.e. mature birch forest) at 100–150 m above sea level, which is the altitude where winter moth outbreaks typically occur (Tenow 1972). At every 200 m along the transects we established permanent sampling stations (i.e. *n* = 10 per transect), where we estimated the density of the local winter moth populations. Density estimates were obtained by counting all larvae on 10 arm-length birch twigs per sampling station, collected haphazardly from different trees within a radius of 20 m of the station point. Each twig was beaten thoroughly with a stick over a large plastic box until all larvae had

detached from the twig and had fallen into the cage. The mean number of larvae per twig then served as a station-specific measure of population density. Both transects in one pair of sites were sampled during a single day and all sites/transects were sampled during 1 week. Sampling was conducted during the four summers in the period 1999–2002 and the sampling time varied somewhat from late June or early July, depending on the phenology in the different years. Care was taken to perform the sampling when most of the larvae were in their 3–4 instars to avoid overlooking the youngest instars during sampling (i.e. the very small 1 instar larvae) or losing late instar larvae (e.g. 5 instar larvae) that had pupated.

Results

Both winter moth and autumnal moth were present on all sites. Here we present data for the winter moth only, because this species predominated in our material. The winter moth already occurred at very low densities (i.e. mean number of larvae per birch twig < 1 at all stations) during the first summer at six sites (Rekvik, Vengsøy, Dåvøy, Karlsøy, Lyngen and Årøy) (Fig. 1, Table 1). The population densities at these low-density sites did not change notably during the next three summers (Table 1). There was a tendency for the low-density sites to be located on the islands; five of the six islands were at low density, while only one of six continental sites had similarly low densities (Fig. 1).

Of the six sites with at least some local populations with more than one larva per birch twig in 1999, there was one site (Reinøya) with populations that on average exhibited a weak increasing trend over the study period (Fig. 1). At the five other sites the winter moth populations were obviously crashing from peak densities during the course of the study period. The populations at one of the crashing sites (Dåfjord) were probably in the very late crash phase in 1999 and reached the same low densities as the six low-density sites the next summer. The four remaining sites (Sandvik, Tussøy, Tromvik and Skulsfjord) still had some increasing populations in 1999 (Fig. 1) that reached peak population densities (> 10 larvae per twig) in 2000. Most populations had entered the crash-phase by the summer of 2001. Three of the peaking/crashing sites were located on the large island Kvaløy (Fig. 1). The cross-correlation coefficients between the Kvaløy sites being connected by continuous birch forest averaged 0·93 (SD = 0·02). In contrast, cross-correlation coefficients (lag zero) between sites on different islands (i.e. sites with habitat barriers between them) averaged 0·04 (SD = 0·53).

Because the study period included both peak and the crash phases at four sites we analyse the spatio-temporal dynamics within these sites in greater detail. The other sites were not subject to such a detailed analysis because there were no significant changes between most of the years (Table 1). Among the four peaking/

Table 1. Mean $\log_e$-transformed densities [$\log_e(N + 1)$] and per capita growth rates ($r = \log_e[N_{t+1} + 1]/\log_e[N_t + 1]$) for the 12 study sites (transects). Standard deviations are in brackets

| Site		1999	2000	2001	2002
Tussøy	$\log(N + 1)$	3·15 (1·18)	2·94 (1·39)	1·05 (1·37)	0·21 (0·47)
	r	−0·21 (0·77)	−1·88 (0·85)	−0·85 (1·15)	
Sandvik	$\log(N + 1)$	4·69 (0·27)	4·66 (0·41)	4·16 (0·44)	2·68 (0·47)
	r	−0·03 (0·39)	−0·50 (0·26)	−1·49 (0·51)	
Tromvik	$\log(N + 1)$	4·22 (0·56)	4·45 (0·74)	3·93 (0·76)	2·81 (0·97)
	r	0·23 (0·30)	−0·52 (0·38)	−1·12 (0·43)	
Skulsfjord	$\log(N + 1))$	4·17 (0·42)	4·33 (0·32)	2·68 (0·61)	0·65 (0·68)
	r	0·16 (0·34)	−1·65 (0·39)	−2·02 (0·50)	
Dåfjord	$\log(N + 1)$	2·33 (0·62)	0·07 (0·62)	0·28 (0·36)	0·54 (0·60)
	r	−2·26 (0·69)	0·21 (0·85)	0·26 (0·71)	
Dåvøy	$\log(N + 1)$	0·61 (0·56)	0·00 (0·00)	0·29 (0·48)	0·32 (0·43)
	r	−0·61 (0·56)	0·29 (0·48)	0·03 (0·53)	
Reinøy	$\log(N + 1)$	2·48 (0·78)	2·53 (1·05)	2·92 (0·56)	2·74 (0·53)
	r	0·05 (0·78)	0·39 (0·76)	−0·18 (0·36)	
Rekvik	$\log(N + 1)$	0·72 (0·86)	0·50 (0·70)	0·50 (0·46)	0·80 (0·53)
	r	−0·22 (0·44)	0·00 (0·48)	0·30 (0·52)	
Vengsøy	$\log(N + 1)$	1·70 (0·61)	0·46 (0·53)	0·64 (0·56)	0·39 (0·43)
	r	−1·25 (0·95)	0·18 (0·76)	−0·25 (0·85)	
Karlsøy	$\log(N + 1)$	0·55 (0·44)	0·66 (0·54)	0·14 (0·44)	0·86 (0·39)
	r	0·10 (0·85)	−0·52 (0·83)	0·72 (0·52)	
Lyngen	$\log(N + 1)$	0·00 (0·00)	0·14 (0·29)	0·00 (0·00)	0·07 (0·22)
	r	0·14 (0·29)	−0·14 (0·29)	0·07 (0·22)	
Årøy	$\log(N + 1)$	0·00 (0·00)	0·00 (0·00)	0·00 (0·00)	0·07 (0·22)
	r	0·00 (0·00)	0·00 (0·00)	0·07 (0·22)	
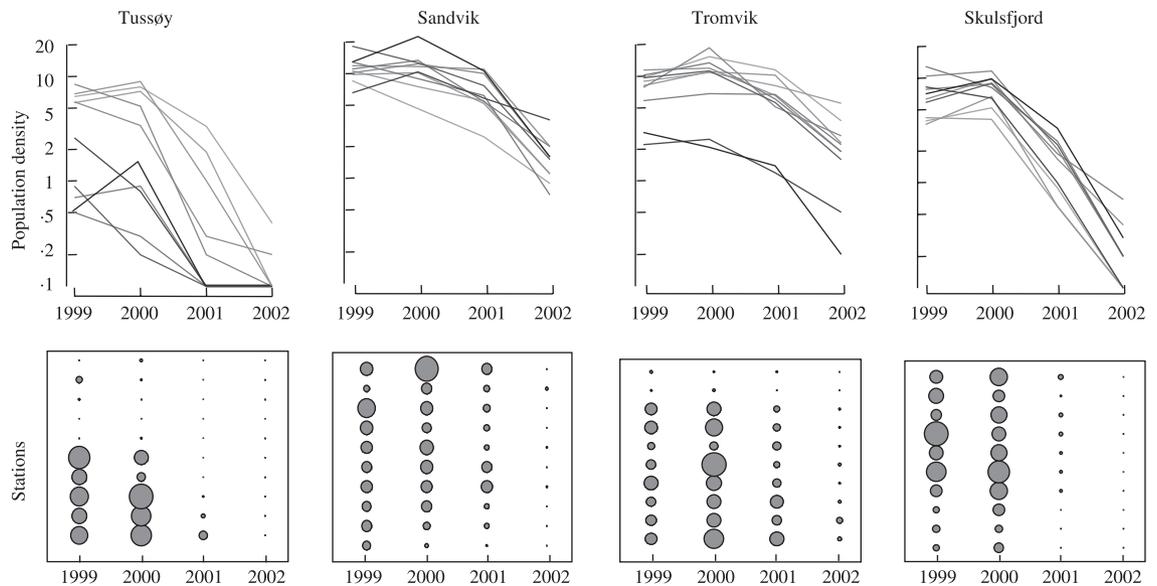
Fig. 2. Spatio-temporal dynamics on four sites where local populations crashed from peak densities during the course of the study. Upper panels: trajectories of population density (number of larvae per birch twig) on a logarithmic scale. Adjacency of populations (= sampling stations) along the transect at each site is indicated by similar thickness and shading of lines. Lower panel: the spatial pattern of local population densities along the transects in the different years. The size of the bubbles denotes the relative local larval densities.

crashing sites, the island site (Tussøy) was in the most advanced stage of the crash, as some of the populations were already close to minimum densities in 1999 (Fig. 2) and the mean rate of change between 1999 and 2000 was negative (Table 1). Within-site variation in population dynamics was also clearly largest at Tussøy (Table 1, Fig. 2). This variation seemed to be spatially structured in the sense that there was a tendency for the

populations in one half to crash before the other half (Fig. 2). We used local polynomial regression models [Cleveland, Grosse & Shyu 1992; function 'loess' implemented in R (Ihaka & Gentleman 1996)] to fit smoothed correlograms to pairwise cross-correlation coefficients (lag zero) of sampling station specific population densities for each transect. We chose a large degree of smoothing (alpha = 1·5) to emphasize patterns at
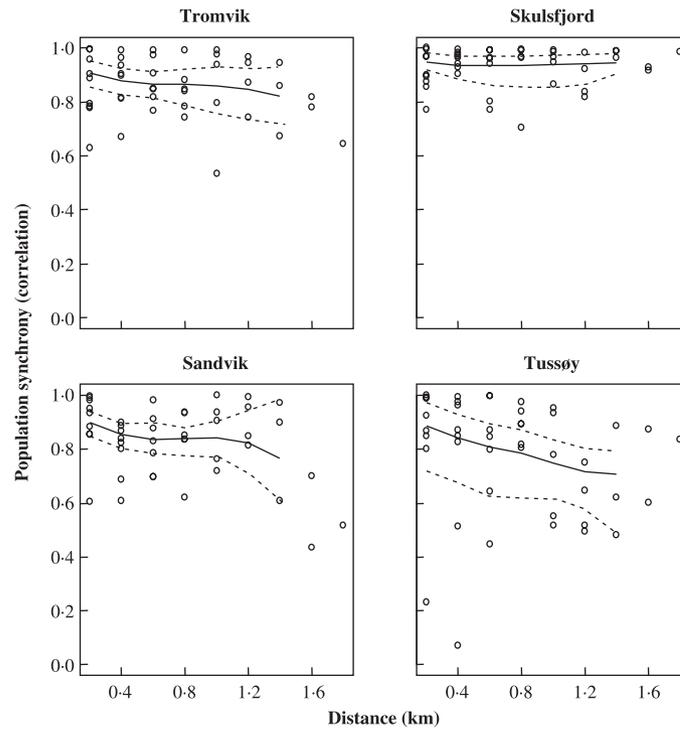
Fig. 3. The degree of spatial synchronous population rate of change [$\log(N_{t+1} + 1)/N_t + 1)$] as a function of distance between local populations at the four study sites (= 1·8 km transects) undergoing population crashes. Dots are cross-correlation coefficients between pairs of populations (= sampling stations along the transect). The curves depicting the relations between synchrony and distance (correlograms) were obtained from local regression models. 5% and 95% confidence envelopes of the predicted curves are given. Predictions for the two most distant correlations were not made because of few data. See main text for further computational details.

the transect level. Confidence envelopes for the local regression curves were estimated by bootstrapping sampling stations 1000 times and using the 5% and 95% quantiles of the distributions of the predicted values (obtained using the 'pred.loess' function). The correlograms indicated that local populations crashed fairly synchronously across the entire transects at all four sites (Fig. 3). The crashes appeared most synchronous at the site Skulsfjord, where the crash was particularly steep (Table 1, Fig. 2). The more spatially variable dynamics at Tussøya were indicated by a somewhat clearer tendency for a decaying synchrony with distance and wider confidence envelopes than the other sites (Fig. 3).

Discussion

The 12 sites studied had winter moth populations with very different population densities and dynamics, although the habitat appeared to be similar, i.e. mature coastal birch forest. There are two possible explanations for this. The first could be that the various sites have qualitatively different population dynamics, i.e. some sites harbour populations with the typical cyclic dynamics of the type described previously from northern Fennoscandia, while other sites could have relatively low and stable population densities, which is a type of dynamics believed previously to be found only at much lower latitudes in Fennoscandia (e.g. Klemola *et al.* 2002). If this kind of fundamentally different local dynamics

at a relatively small scale was the case, the reported large-scale regional pattern of a northern cyclic and southern non-cyclic geometrid moth population dynamics in Fennoscandia (cf. Tenow 1972; Ruohomäki *et al.* 2000; Klemola *et al.* 2002) would be disrupted. The second possibility is that all sites harbour populations with 'normal' northern population cycles, but that the sites were out of phase with each other. Note that both alternatives imply spatially asynchronous dynamics, but the underlying causes would be different.

Although a statistically rigorous evaluation of whether forest Lepidoptera populations are cyclic or stable requires 30–40-year time series (Liebhold & Kamata 2000), we still think it is timely and pertinent to report our findings, and to argue that the cyclic–asynchrony alternative (rather than the stable–cyclic alternative) is the most probable explanation for the observed spatio-temporal dynamics. All sites had population trajectories that are compatible with signatures of cyclic phases as known from the only really long-term quantitative data on the winter moth, i.e. Hogstad's 30-year time series from subalpine central Norway (Hogstad 1997). Four sites in our study had the typical signatures of cyclic peaks and crashes (Skulfjord, Tussøya, Sandvik and Tromvik), one site was in the late phase of the crash entering the low phase (Dåfjord), another site was increasing (Reinøy) and, finally, there were six sites that were compatible with low-phase dynamics (Rekvik, Vengsøy, Dåvøy, Karlsøy, Årøy, Lyngen). In particular,

low-phase winter moth populations may stay at very low densities without notable growth for 3–4 years after the crash phase has been completed (Roland 1994; Hogstad 1997). A high frequency of recently dead birch twigs and old leaves with the typical signs of gnawing at the six low-density sites, as well as information from local people who are very well aware of the outbreak dynamics of 'lauvmakk' (the local common name for winter moth larvae), indicated that outbreak densities had been prevalent 1 or a few years before.

The cyclic phase differences between sites we infer from our data imply that some of them were maximally out of phase with each other. In fact, some of the most distinct population-phase differences were evident within continent–island pair constellations where the sites were separated by only 5 km (e.g. Tromvik vs. Rekvik, where Rekvik had entered the low phase before the onset of our study, while Tromvik reached the same phase 4 years later; Fig. 1).

The common notion that geometrid moth populations have the same synchronous dynamics throughout northern Fennoscandia stems mainly from Tenow (1972). Tenow's survey differs from our study design in several respects. However, most important in the context of spatial population dynamics is that it encompasses a much larger scale with a low spatial resolution so that discrepancies from large outbreaks in a given period and a specific region could easily go unnoticed. Tenow himself acknowledges succinctly that the nature of qualitative survey data gathered from a variety of sources will tend to blur details about the dynamics that go beyond the years and locations with large outbreaks. More recent quantitative time series on geometrid moth dynamics in Fennoscandia stem either from single sites (Hogstad 1997; Selås *et al.* 2001) or have examined spatial aspects of the dynamics at the forest stand level (Bylund 1997; Ruohomäki *et al.* 1997), or topographic-related variation in lethal winter temperatures for eggs of the autumnal moth (Niemelä 1979; Virtanen, Neuvonen & Nikula 1998).

Our demonstration of a pronounced population asynchrony in the winter moth also contrasts with several recent studies of a number other cyclic moth species in forest ecosystems outside Fennoscandia (Barbour 1988; Myers 1988, 1998; Swetnam & Lynch 1993; Williams & Liebhold 1995, 2000; Peltonen *et al.* 2002). These studies, based on statistical analyses of region-wide, relatively high-resolution surveys of defoliation patterns of economically important species, have shown convincingly that the extent of spatial synchrony is typically larger (> 400 km), i.e. much larger than the extent of the area encompassed in the present study. It has been concluded that external disturbance in terms of climatic anomalies (i.e. the Moran effect, Moran 1953) is the most probable cause behind the large-scale synchrony (Berryman 1996; Myers 1998; Peltonen *et al.* 2002). In the case of geometrid moths of the sub-Arctic birch forests in northern Fennoscandia, large-scale climatic events have also been forwarded as

the most probable synchronizing agent (Tenow 1972; Ruohomäki *et al.* 2000; Tanhuanpää *et al.* 2002). Lethal winter temperature is a particularly likely candidate in this context, as it has been shown to affect the topographic distribution of northern inland populations of autumnal moth in Finland (Virtanen *et al.* 1998). However, unusual spring weather causing a mismatch between larval and host (i.e. birch) phenology (Ruohomäki *et al.* 2000; Visser & Holleman 2001) as well as high summer temperatures without any particular mechanism specified (Niemelä 1980) has also been suggested as a potential synchronizing factor. In the case of our coastal study area, being ruled by an oceanic climate the temperature never drops even close to what is lethal for winter moth eggs. At Lyngseid meteorological station, adjacent to our most continental sites at Lyngen and Årøy, the mean January temperature is −4·5 °C, while it is −1·9 °C at Sommarøy adjacent to our most oceanic sites at Tussøy and Sandvik (Norwegian Meteorological institute website). In any case, the corresponding July temperatures at the same stations are 11·9 °C and 12·5 °C. The distinct asynchrony between adjacent sites (< 10 km apart) clearly belonging to the same climatic domain rules out the possibility that climate or, for that matter, any other supposedly large-scale phenomenon such as mast-seed years (Selås *et al.* 2001), could be responsible for the observed population phase differences.

As well as climatic variation, dispersal and interactions with natural enemies have been regarded as the two other main determinants of the degree of spatial synchrony of cycling populations (Bjørnstad *et al.* 1999; Koenig 1999; Lundberg *et al.* 2000). These biotic factors are both connected to the mobility of individuals (either of the species in question or its enemy) and are often assumed to operate on a smaller spatial scale than regionalized factors such as climate (e.g. Sutcliffe *et al.* 1996; Peltonen *et al.* 2002). Because adult female winter moths are not able to fly, dispersal must take place through ballooning in first instar larvae. Although ballooning larvae of the winter moth have been shown to be able to disperse several hundred metres (Edland 1971), ballooning is generally thought to be poorly effective beyond the forest-stand scale in forest Lepidoptera (Ruohomäki *et al.* 2000). Nothing is known about the extent of dispersal of important enemies such as insect parasitoids, although they have been assumed to be weak fliers (Virtanen & Neuvonen 1999). As an essential part of our study design we included open stretches of sea that we expected would be efficient barriers to dispersal both for winter moths and their most important enemies (e.g. parasitic Hymenoptera and predatory shrews). Accordingly there were several cases of a pronounced asynchrony between continent–island pairs. That lack of habitat discontinuity and dispersal barriers might have played a role is also indicated by the fact that the only sites being connected by continuous forest exhibited highly synchronous dynamics, and moreover that local populations were mainly synchronous within sites.

Conclusion

The present study is, to the best of our knowledge, the first that addresses the topic of spatial synchrony of cyclic insect population dynamics by a study design targeted specifically for shedding light into the underlying mechanisms. Although our study still is relatively short-term, we have already evidence for distinct population-phase differences between localities in prime moth habitats (i.e. mature birch forest) being separated by only a few kilometres. Our findings thus contrast with the common notion that geometrid moths in sub-Arctic birch forests exhibit large-scale synchrony. They also contrast with recent analyses of cyclically outbreaking insects in other forest ecosystems, which invariably have estimated synchrony domains to extend beyond the scale of our study area (e.g. Peltonen *et al*. 2002). The most pronounced cases of asynchrony in our study were found between sites on nearby islands with exactly the same climate, but where open stretches of sea between sites presumably acted as efficient barriers for dispersal in both moths and their enemies. This suggests that biotic mechanisms may play a pivotal role for the resultant spatio-temporal dynamics.

Our study highlights the value of specifically dedicated designs in the study of spatio-temporal population dynamics. Such studies, even though they are relatively short-term, can provide stronger inferences about what are the underlying mechanisms than untargeted surveys, which typically have formed the basis for most previous studies on this topic.

Acknowledgements

References

Adler, G.H. (1994) Tropical forest fragmentation and isolation promote asynchrony among populations of a frugivorous rodent. *Journal of Animal Ecology*, **63**, 903–911.

Barbour, A.D. (1988) Synchronous fluctuations in spatially separated populations of cyclic forest insects. *Population Dynamics of Forest Insects* (eds A.D. Watt, S.R. Leather, M.D. Hunter & N.A.C. Kidd), pp. 339–346. Intercept, Andover.

Bascompte, J. & Solé, R.V. (1998) *Modelling Spatiotemporal Dynamics in Ecology*. Springer-Verlag, Berlin.

Berryman, A.A. (1996) What causes population cycles of forest Lepidoptera? *Trends in Ecology and Evolution*, **11**, 28–32.

Bjørnstad, O.N. (2000) Cycles and synchrony: two historical 'experiments' and one experience. *Journal of Animal Ecology*, **69**, 869–873.

Bjørnstad, O.N., Ims, R.A. & Lambin, X. (1999) Spatial population dynamics: analyzing patterns and processes of population synchrony. *Trends in Ecology and Evolution*, **14**, 427–432.

Bondrup-Nielsen, S. & Ims, R.A. (1988) Demography during a population crash of the wood lemming, *Myopus schisticolor*. *Canadian Journal of Zoology*, **66**, 2442–2448.

Bylund, H. (1997) Stand age-structure influence in a low population peak of *Epirrita autumnata* in a mountain birch forest. *Ecography*, **20**, 319–326.

Bylund, H. (1999) Climate and the population dynamics of two insect outbreak species in the north. *Ecological Bulletins*, **47**, 54–62.

Cleveland, W.S., Grosse, E. & Shyu, W.M. (1992) Local regression models. *Statistical Models in S* (eds J.M. Chambers & T.J. Hastie), pp. 309–325. Wadsworth & Brooks, Cole.

Edland, T. (1971) Wind dispersal of the winter moth *Operophtera brumata* L. (Lep., Geometridae) and its relevance to control measures. *Norsk Entomologisk Tidskrift*, **18**, 103–105.

Erlinge, S., Danell, K., Frodin, P., Hasselquist, D., Nilsson, P., Olofsson, E.B. & Svensson, M. (1999) Asynchronous population dynamics of Siberian lemmings across the Palaearctic tundra. *Oecologia*, **119**, 493–500.

Grenfell, B.T., Wilson, K., Finkenstädt, B.F., Coulson, T.N., Murray, S., Albon, S.D., Pemberton, J.M., Clutton-Brock, T.H. & Crawley, M.J. (1998) Noise and determinism in synchronized sheep dynamics. *Nature*, **394**, 674–677.

Hanski, I. & Woiwod, I.P. (1993) Spatial synchrony in the dynamics of moth and aphid populations. *Journal of Animal Ecology*, **62**, 656–668.

Hansson, L. & Henttonen, H. (1988) Rodent dynamics as community processes. *Trends in Ecology and Evolution*, **3**, 195–200.

Haukioja, E., Neuvonen, S., Hanhimäki, S. & Niemelä, P. (1988) The autumnal moth in Fennoscandia. *Dynamics of Forest Insect Populations: Patterns, Causes and Management Strategies* (ed. A.A. Berryman), pp. 163–177. Academic Press, New York.

Hawkins, B.A. & Holyoak, M. (1998) Transcontinental crashes of insect populations? *American Naturalist*, **152**, 480–484.

Hogstad, O. (1997) Population fluctuations of *Epirrita autumnata* Bkh. & *Operophtera brumata* (L.) (Lep., Geometridae) during 25 years and habitat distribution of their larvae during a mass outbreak in a subalpine birch forest in Central Norway. *Fauna Norvegica Serie B*, **44**, 1–10.

Hudson, P.J. & Cattadori, I.M. (1999) The Moran effect: a cause of population synchrony. *Trends in Ecology and Evolution*, **14**, 1–2.

Ihaka, R. & Gentleman, R. (1996) R: a language for data analysis and graphics. *Journal of Computational and Graphical Statistics*, **5**, 299–314.

Kendall, B.E., Bjørnstad, O.N., Bascomte, J., Keith, T. & Fagan, W. (2000) Ecological interactions, environmental correlation and spatial synchrony. *American Naturalist*, **155**, 674–677.

Klemola, T., Tanhuanpää, M., Korpimäki, E. & Ruohomäki, K. (2002) Specialist and generalist natural enemies as an explanation for geographical gradients in population cycles of northern herbivores. *Oikos*, **99**, 83–94.

Koenig, W.D. (1999) Spatial autocorrelation of ecological phenomena. *Trends in Ecology and Evolution*, **14**, 22–26.

Krebs, C.J., Zimmerling, T.N., Jardine, C., Trostel, K.A., Kenney, A.J., Gilbert, S. & Hofer, E.J. (2002) Cyclic dynamics of snowshoe hares on a small island in the Yukon. *Canadian Journal of Zoology*, **80**, 1442–1450.

Laakkonen, J., Fisher, R.N. & Case, T.J. (2001) Effect of land cover, habitat fragmentation and ant colonies on the distribution and abundance of shrews in southern California. *Journal of Animal Ecology*, **70**, 776–788.

Liebhold, A. & Kamata, N. (2000) Introduction: are population cycles and spatial synchrony an universal characteristics forest insect populations? *Population Ecology*, **42**, 205–209.

Lundberg, P., Ranta, E., Ripa, J. & Kaitala, V. (2000) Population variability in space and time. *Trends in Ecology and Evolution*, **15**, 460–464.

Moran, P.A.P. (1953) The statistical analysis of the Canadian lynx cycle. II. Synchronization and meteorology. *Australian Journal of Zoology*, **1**, 291–298.

Myers, J.H. (1988) Can a general hypothesis explain population cycles of forest Lepidoptera? *Advances in Ecological Research*, **18**, 179–242.

Myers, J.H. (1998) Synchrony in outbreaks of forest Lepidoptera: a possible example of the Moran effect. *Ecology*, **79**, 1111–1117.

Neuvonen, S., Niemelä, P. & Virtanen, T. (1999) Climatic change and insect outbreaks in boreal forests: the role of winter temperatures. *Ecological Bulletins*, **47**, 63–67.

Niemelä, P. (1979) Topographical delimitation of *Oporinia*-damages: experimental evidence of the effect of winter temperature. *Reports from the Kevo Subarctic Research Station*, **15**, 33–36.

Niemelä, P. (1980) Dependence of *Oporinia autumnata* (Lep., Geometridae) outbreaks on summer temperature. *Reports from the Kevo Subarctic Research Station*, **16**, 27–30.

Paradis, E., Baillie, S.R., Sutherland, W.J. & Gregory, R.D. (2000) Spatial synchrony in populations of birds: effects of habitat, population trend, and spatial scale. *Ecology*, **81**, 2112–2125.

Peltonen, M., Liebhold, A.M., Bjørnstad, O.N. & Williams, D.W. (2002) Spatial synchrony in forest insect outbreaks: roles of regional stochasticity and dispersal. *Ecology*, **83**, 3120–3129.

Ranta, E., Kaitala, V. & Lundberg, P. (1998) Population variability in space and time: the dynamics of synchronous population fluctuations. *Oikos*, **83**, 376–382.

Roland, J. (1994) After the decline – what maintains low winter moth densities after successful biological control. *Journal of Animal Ecology*, **63**, 392–398.

Ruohomäki, K., Tanhuanpää, M., Ayres, M.P., Kaitaniemi, P., Tammaru, T. & Haukioja, E. (2000) Causes of cyclicity of *Epirrita autumnata* (Lepidoptera, Geometridae): grandiose theory and tedious practice. *Population Ecology*, **42**, 211–223.

Ruohomäki, K., Virtanen, T., Kaitaniemi, P. & Tammaru, T. (1997) Old mountain birches at high altitudes are prone to outbreaks of *Epirrita autumnata* (Lepidoptera: Geometridae). *Ecological Entomology*, **26**, 1096–1104.

Selås, V., Hogstad, O., Andersson, G. & von Proschwitz, T. (2001) Population cycles of autumnal moth, *Epirrita autumnata*, in relation to birch mast seeding. *Oecologia*, **129**, 213–219.

Steen, H., Ims, R.A. & Sonerud, G.A. (1996) Spatial and temporal patterns of small-rodent population dynamics at a regional scale. *Ecology*, **77**, 2365–2372.

Sutcliffe, O.L., Thomas, C.D. & Moss, D. (1996) Spatial synchrony and asynchrony in butterfly population dynamics. *Journal of Animal Ecology*, **65**, 85–95.

Swetnam, T.W. & Lynch, A.M. (1993) Multicentury, regional-scale patterns of western spruce budworm outbreaks. *Ecological Monographs*, **63**, 399–424.

Tanhuanpää, M., Ruohomäki, K., Turchin, P., Ayres, M.P., Bylund, H., Kaitaniemi, P., Tammaru, T. & Haukioja, E. (2002) Population cycles of the autumnal moth in Fennoscandia. *Population Cycles: the Case for Trophic Interactions* (ed. A. A. Berryman), pp. 142–154. Oxford University Press, Oxford.

Tenow, O. (1972) The outbreaks of *Oporinia autumnata* Bkh. & *Operophtera* spp. (Lep., Geomtridae) in the Scandinavian mountain chain and northern Finland 1862–1968. *Zoologiska Bidrag Från Uppsala Supplement*, **2**, 1–107.

Tenow, O. (1996) Hazards to a mountain birch forest – Abisko in perspective. *Ecological Bulletins*, **45**, 104–114.

Virtanen, T. & Neuvonen, S. (1999) Performance of moth larvae on birch in relation to altitude, climate, host quality and parasitoids. *Oecologia*, **120**, 92–101.

Virtanen, T., Neuvonen, S. & Nikula, A. (1998) Modelling topoclimatic patterns of egg mortality of *Epirrita autumnata* (Lepidoptera: Geometridae) with a geographical information system: predictions for current climate and warmer climate scenarios. *Journal of Applied Ecology*, **35**, 311–322.

Visser, M.E. & Holleman, L.J.M. (2001) Warmer springs disrupt the synchrony of oak and winter moth phenology. *Proceedings of the Royal Society London B*, **268**, 289–294.

Williams, D.W. & Liebhold, A.M. (1995) Influence of weather on the synchrony of gypsy moth (Lepidoptera, Lymantriidae) outbreaks in New England. *Environmental Entomology*, **24**, 987–995.

Williams, D.W. & Liebhold, A.M. (2000) Spatial synchrony of spruce budworm outbreaks in eastern North America. *Ecology*, **81**, 2753–2766.